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AN OUTLINE OF THE ECOLOGY OF GYRINIDAE.

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I. ADAPTATIONS.

General aquatic adaptations: The adaptations to an aquatic environment to be found in the Gyrinidae are much the same as those described by Sharp (1882) and Needham and Williamson (1907, p. 482–485) for the Dytiscidae, to which they are probably genetically related. These are (1) a stream line form offering a minimum of resistance to the water, (2) increased rigidity, and (3) natatorial legs.

The first is manifested in the continuous outline of the head, prothorax, and elytra, by the depression of the eyes, the absence of pubescence and sculpture, and the depression of parts of the venter. When not in use, the legs are received in more or less pronounced grooves.

Increased rigidity is brought about in part by an anterio-posterior compression and the overlapping of parts, effected by the deep immersion of the head in the prothorax and by the coadaptation of prothorax and mesothorax. The prothorax overlaps the mesothorax except in the midventral region where the anterior lobe of the mesosternum protrudes between the procoxae, which are themselves received in hollows on the anterior aspect of the mesosternum. The mesofurcae protrude caudad through the anterior foramen of the mesothorax, where they serve as points of attachment for muscles and add to the general rigidity.

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The mechanism involved in locking the elytra must be considered a general coleopterous structure rather than a special gyrinid or even a special aquatic adaptation. It provides a definite air space between the elytra and the dorsum of the abdomen in immediate contact with the abdominal spiracles. The metaspiracles are situated on the metacoria between the metaepisternum and the mesoepimeron and are in a position to draw their air supply from the same source.

The meso- and metapods are both adapted for swimming, apparently acting as powerful paddles. They represent a much higher degree of aquatic adaptation than do the legs of any other aquatic Coleoptera. Due to the fact that the mesopods as well as the metapods are natatorial, both meso- and metacoxae are solidly and deeply set in the venter of the body, and, with the meso- and metasternum, are well developed for containing the powerful muscles that operate the legs, a considerable advance over *Dytiscus.* The propods function (1) as ambulatory appendages on land, (2) as prehensile appendages, (3) as clasping appendages for the male during copulation, and (4) (Sharp, 1869, p. 53) as steering organs. Wesenberg-Lund (1915, p. 304) suggests that the genital lobes may be extruded and serve as rudders.

Adaptations to surface film: In addition to their general aquatic adaptations which they have to an extent in common with the Dytiscidae, the Gyrinidae have a series of features that adapt them to conditions on the surface of the water.

Dineutus floats in the water like a boat rather than rests on it like a water-strider. Due to an air store the body of the beetle is lighter than water, so that, when the animal is submerged, it must cling to something in order to maintain a position at rest beneath the surface. Likewise, when swimming under water, the beetle must move forward with its anterior end slightly bent down. When the beetles were placed on the surface of the water in a plane sided glass aquarium and the water was illuminated by a single source of light arranged so that the beam of light passed through the wall of the aquarium below the surface of the water, the ventral surface of the gyrinids was distinctly visible, air bubbles were seen clinging to it, and an image of the venter was clearly reflected by the surface film. When the angle of incidence of a beam of light passing from water into air exceeds 48° 35′ none of the light passes through the surface film but is reflected in total. If the lower surface of the beetle had been covered by an air film, it would have appeared with the same sil-

very sheen when viewed from below as did the few bubbles of air left clinging to the ventral surface. Moreover, unless the surface film was actually broken by the venter, it would not have been reflected in the film.

The surface film is of some assistance in keeping the animal afloat. As the beetle rests on it, it appears to be depressed slightly on all sides, offering a measure of support to the body. The importance of this support was demonstrated by the difficulty that the animal experienced in keeping afloat when the surface tension of the water was reduced by the introduction of a few drops of liquid soap. Especially in the region of the head the water line rose considerably. The beetles recovered their equilibrium when they were taken out of the water into which the soap had been introduced, allowed to dry, and returned to normal conditions.

The water line is normally maintained along the lateral margins of the elytra and epinotum and, on the head, along the supraocular ridge, the bristles that fringe the auricular lobe of the antennal pedicel, the lateral margin of the postclypeus, and the lateral and anterior margins of the labrum. The lower eye is completely submerged, but appeared to be covered with a film of air that would limit but not eliminate the eye as an organ of vision beneath the surface.

The ommatidia of the compound eye are of such a structure as to be stimulated primarily if not entirely by rays of light striking the eye at very close to a right angle to its general surface (Folsom, 1922, p. 98). Such rays of light are least likely to be interfered with by an air film over the surface of the eye, for a ray of light striking a surface film at right angles passes through with no deflection and a minimum of reflection. Rays of light striking the eye obliquely and hence entirely reflected or refracted by the surface film are the very ones that, even though they impinged upon the eye unmodified, would stimulate it little or not at all. The presence of the surface film does reduce, at least theoretically, the amount of light reaching the individual facets of the eye and, hence, the eye as a whole. In fact it limits by nearly one half (41.25/90 or 45.8 1/3 per cent.) the amount of light other than that reaching the surface of the facet at exactly right angles to it. This follows from the circumstance that the angle of refraction increases twice as fast as the angle of incidence. The inferior eye has a considerably greater area than the dorsal eye and thus in a measure compensates for the possible decrease in the amount of light received. Miall's fear (1895, p. 34) about

the uselessness of the ventral eye is quieted; Sharp's (1869, p. 521) suspicion is confirmed.

The water line extends ventrad to the club of the antenna so that, when swimming on the surface, the club is held in the air. The fringe of hairs on the margin of the auricular lobe of the antennal pedicel serves to maintain the water line at this point and to prevent it from infringing upon the club. The antennae of *Dineutus* that were scrutinized while their owners were submerged were seen to be fully expanded, with a bubble of air surrounding the basal part of the club. This bubble was probably held in place by the auricular lobe and the fringe of hairs bordering it. It was impossible to determine the presence of an air film covering the apex of the club that projected beyond the bubble. Perhaps it is unwettable, so that immediately upon reemerging it is entirely dry. There is no evidence that the auricular lobe closes over the club (*cf.* Miall, 1895, p. 34).

The observations made on *Dineutus* were in part repeated and in no instance refuted on *Gyrinus*. There is reason to believe that these relationships are applicable to the family as a whole.

II. Habitat.

Imago: The habitat of adult Gyrinidae is the surface of fresh standing water and streams never very far from shore or aquatic vegetation of some sort. In the absence of data concerning the exotic species, it is impossible to make any certain generalizations. I suspect that the primitive habitat was the surface of standing water, and should ascribe to this habitat the generality of species of *Enhydrus, Dineutus, Androgyrus, Macrogyrus, Aulonogyrus,* and *Gyrinus*. Most of the Orectochilini appear to be stream inhabitants, and among the Enhydrini *Porrhorrhynchus* and certain *Dineutus*.

(1) Quiet water habitat. Gyrinids do not go many feet from vegetation. I have found *Dineutus americanus* L., *nigrior* Rbts., and *hornii* Rbts. on ponds and lakes in Michigan, and the same habitat is reported for *americanus* L. (Wilson, 1923, p. 306), *emarginatus* Say (Blatchley, 1910, p. 241), *metallicus* Aubé (Ochs, 1924, p. 5). Nowrojee (1912, p. 177) records *D. unidentatus* Aubé in India from the river during hot weather and from ponds and pits filled in by rain during the monsoons. Mr. F. M. Gaige found *D. truncatus* Sharp and *Gyrinus parcus* Say on the surface of a series of heavily shaded pools in the bed of a dry stream in Panama. Nowrojee's record suggests the possibility that *truncatus* is a river inhabitant during the wet season.

The species of *Gyrinus* seem to be more ubiquitous than *Dineutus.* They live on ponds and lakes, but likewise they do not hesitate to frequent the water of ditches, bog pools, swamps, and small protected coves along the margins of slowly flowing streams, and they have been seen swimming on a side-walk puddle or in a horse trough. *G. marinus* Gyll. of Europe inhabits "sussem u. Brakwasser" (Schaufuss, 1916, p. 143). Wilson (1923, p. 309) claims that *Gyrinus* prefers gently running water and his figure (1923, p. 5) shows a swarm of them on the downriver side of a boat wharf, but in a position protected from the current. I am inclined to doubt whether *Gyrinus* ever lives in the current. I have seen numerous swarms along the margin of streams, but they have always been in little coves where the current was imperceptible, and I suspect that this is the interpretation to be placed upon Wilson's record. Fall (1901, p. 55) says that in California *G. plicifer* occurs in small streams while *consobrinus* prefers larger and more permanent waters, but adds nothing more.

(2) Stream habitat. *Dineutus discolor* Aubé is the only stream gyrinid that has come under the direct observation of the author. This species apparently inhabits only the open flowing water of slowly moving streams or the slowly flowing portions of swifter streams (Blatchley, 1910, p. 241; T. H. Hubbell; J. W. Angell). The beetles swim in the current and are often gregarious. They head upstream and swim in a series of jerks only just fast enough to maintain a position that is fixed relative to the shore line. Individual beetles occasionally come nearer shore where the current is less swift, and here they swim about in the irregular fashion of their quiet water relatives. When alarmed, they dart off a meter or so down stream and then dive and cling to submerged objects. In the course of a few moments they have begun to reassemble in the same spot. At one place, about 14 meters below the situation occupied by the *D. discolor* and in a typical pond situation which was in direct communication with the stream occurred *D. nigrior* and *D. hornii,* but no *D. discolor,* showing the completely different habitat preference of the two groups of species. When specimens of *D. discolor* were brought into the laboratory they seemed to thrive as well on the standing water of the aquarium as did the quiet water species. Since writing the above, I have found *D. productus* Rbts., heretofore known only from Texas and Louisiana, in the current of the Sangamon River, at Decatur, Ill.

The stream habitat is indicated in the literature for the following: *Dineutus serrulatus* Lec. (Blatchley, 1919, p. 316; Dozier, 1920, p. 362), *D. longimanus portoricensis* Ochs (Ochs, 1924, p. 6), *D. vittatus* (Germ.) (W. J. Clench, J. W. Angell), *D. robertsi* Leng (Leng, 1911, p. 11), possibly *D. truncatus* Sharp (F. M. Gaige) and *D. unidentatus* Aubé (Nowrojee, *ibid.*), *Porrhorrhynchus* (Régimbart, 1902, p. 5; 1907, p. 153), Orectochilini (Sharp, 1868, p. 59–60, 1882, p. 50–51; Kolbe, 1880, p. 228; Régimbart, 1884, p. 382–384, 1902, p. 8–10; Reitter, 1908, p. 237; Schaufuss, 1916, p. 141–143; de Kerherve, 1922, p. 36; Nowrojee, 1912, p. 180; Leconte, 1868, p. 373; though the lake habitat is indicated at times for *Orectochilus villosus* O. Mull.) Wesenberg-Lund, 1913, p. 239; Sharp, 1868, p. 59–60). If body form is any indication of habitat, *Dineutus angustus* Lec. is a stream species. There is some evidence that the habitats of *Orectochilus villosus* and *Gyrinus natator* are mutually exclusive, the one on running water, the other on quiet water (de Kerherve, 1922, p. 36).

Larvae: The larvae are gill-breathers and independent of the surface, so are able to escape the limitations to which dytiscid larvae are subject. In Third Sister Lake, a small lake near Ann Arbor, Michigan, inhabited by immense numbers of *Gyrinus* and *Dineutus nigrior* and *hornii,* nearly fully grown *Dineutus* larvae were found in beds of completely submerged vegetation (water grass and elodea). There were from one to three or four feet of open water between the top of the elodea and the surface of the lake. No other beetle larvae and no air breathing insects, larvae or adults were found, with the exception of numerous specimens of the minute dytiscid, *Bidessus flavicollis* (Lec.). Gill breathing insects (Odonata, Trichoptera, Neuroptera) were abundant. Nowrojee (1912, p. 178) found *D. unidentatus* larvae in submerged vegetation likewise. Two younger *Dineutus* larvae were found in Third Sister Lake in somewhat shallower water (12 to 18 inches) nearer the emergent vegetation where eggs had been found, and it is possible that there is a migration of the growing larvae from shallower into deeper water.

Wesenberg-Lund (1913, p. 239; 1915, p. 305) finds *Orectochilus villosus* in lakes. He suggests that the larvae live on the stalks and leaves of the *Potamogeton* in the same locality, often in several meters of water, a situation that resembles that of *Dineutus.* No definite information is at hand concerning *Gyrinus* (*ibid.*).

III. Life History.

In the Gyrinidae the larvae and adults occupy different ecological situations. The larval period is entirely a time of feeding and growth. The adult must reproduce and this involves seeking out the opposite sex, copulation, and oviposition. Probably, too, the adult must feed before laying eggs. The distribution of the species devolves largely upon the adult.

Habits: When undisturbed *Dineutus* and *Gyrinus* gather together in immense schools and either rest or swim slowly over the surface of the water. They are gregarious to a marked degree, though scattered individuals are always to be encountered. The rapid gyrating motion is not their normal means of progression, but is a reaction to an unusual stimulus in the nature of a reflex. The stimulus may be visual, as the movement of a person on the bank, or tactual, as the agitation of the water or contact with an unfamiliar object. Dalgliesh (1912, p. 65) calculated that *Gyrinus* swims about seven hundred and twenty times its own length in a minute. I computed that *Dineutus discolor* swims well over a thousand times its own length in a minute. When alarmed the members of a swarm scatter in all directions. As one approaches a school of *Gyrinus* in a boat the stragglers around the edge of the swarm become aware of the presence of the unusual object and are the first to become disturbed. They dash off in every direction. Those that go towards the rest of the school collide with some of their fellows, which serves to communicate the alarm to them. These immediately collide with others, and these with others, until, in the course of a few seconds, the whole mass is in a condition of panic and is scattering in every direction. The individuals, when alarmed, swim only a few feet, then dive and cling for a few moments to some submerged object, when they begin coming to the surface and reassembling again in the place from which they were driven only a few minutes before.

Wilson (1923, p. 306) notes the habit of *Dineutus* and *Gyrinus* to seek shady places, especially on bright days, and I have observed the same thing. It is especially pronounced in *Gyrinus,* and I have observed a swarm of these carefully congregated in the shade at the same time that the *Dineutus* were swimming freely all over the surface of the small lake. Particularly does a school of *Gyrinus* delight to assemble under some overhanging branch or disport itself in the midst of a partly submerged bush.

In Michigan scattered individuals of *Gyrinus* are frequently

observed in a swarm of *Dineutus* as well as a mixture of *D. nigrior* and *D. hornii* in the same school. Several species of *Gyrinus* frequently occur together in the same swarm (Fall, 1922, p. 270–272; Sharp, 1868, p. 54), though this is not invariable (Lake Superior, Leconte, 1868, p. 373; Frankfurt am Main, Georg Ochs).

The adults drown easily. It was necessary to bring specimens into the laboratory in paper bags or other containers that did not accumulate water at the bottom. Specimens have been kept as long as seven hours in this way without mortality, though after twenty-four hours all the *Dineutus* and over half of the *Gyrinus* were dead.

The beetles fly readily (Osborn, 1886, p. 63; Miall, 1895, p. 32, 162; Wilson, *ibid.*; Fall, 1901, p. 55), and can detect the presence of water at a distance (Weiss, 1914, p. 33–34; Turner, 1924, p. 50–52). Miall (1895, p. 33) notes the odor secreted by the beetles, but this does not seem to protect them entirely against the attack of fish (Wilson, 1923, p. 252–259).

The late appearance of the adults in the fall and their early appearance in numbers in the spring makes it probable that they hibernate as imagoes in the temperate portions of their range (*cf.* Wesenberg-Lund, 1913, p. 239, who remarks that there is a little evidence that *Gyrinus* may hibernate as larvae likewise).

Food: The food is animal matter that has fallen on the surface of the water (Miall, *ibid.*; Wilson, *ibid.*), though Miall found that captive *Gyrinus* could never be induced to eat dead flies, but ate water plants. I have myself induced captive *Dineutus* to feed on dead flies and on bits of raw beef that were made to float by spearing them on toothpicks. Never would they feed unless the meat was at the surface.

Copulation: During copulation the male assumes a position on the back of the female sufficiently caudad to enable him to curve the tip of his abdomen, containing the aedeagus, downward and forward so as to establish contact with the tip of her abdomen, containing the female genitalia. As long as the male retains his position, the burden of locomotion falls on the female. Sharp (1914, p. 130) believes that the lateral lobes of the aedeagus do not enter the female during copula. There is evidence that the sperm is passed to the female in a spermatophore (Régimbart, 1884, p. 383–384; Sharp, *ibid.*).

Gyrinus (Schiödte, 1841, p. 556, quoted by Wesenberg-Lund, 1913, p. 238) and *Dineutus* copulate on the surface of the water,

the males of *Gyrinus* (*ibid.*) often remaining on the females for an entire day. In *Dineutus* (*hornii* and *nigrior* in the daytime in June) the male mounts on the back of the female so that the anterior margin of his head is about a millimeter posterior to the anterior margin of his mate's elytra. With his prothoracic legs he grasps the wing covers of his mate very nearly in the region of the humeri. His mesopods and metapods are not used. The female continues to swim around much as usual, though the actual moment of copula was not observed. A slight stimulus suffices to cause the male to loose his hold. Females laid fertilized eggs as long as three days after separation from the males. *Orectochilus villosus* (Régimbart, *ibid.*) comes to shore for the actual act of copula.

Oviposition: The eggs are laid on submerged vegetation or submerged portions of emergent vegetation (*Dineutus:* Wilson, 1923, p. 302; *Gyrinus:* Schiödte, *ibid.*; Wesenberg-Lund, 1913, p. 238–239). I found the eggs of *Dineutus* (*nigrior* or *hornii*) in June and July laid end to end on the stems of emergent vegetation a few inches below the surface of the water. In captivity during the same months eggs of both *Dineutus* (*nigrior, hornii, discolor*) and *Gyrinus* were laid on aquarium plants and on the sides of the container both above and below the water line. Those laid in the air desiccated. When females were brought from the field and placed in aquaria most of them laid eggs within the first twelve or eighteen hours. From twenty to fifty eggs were usually laid by a single *Dineutus.*

The incubation periods are as follows: *Dineutus americanus* (Wilson, *ibid.*) : 5–6 days; *D. hornii:* 9–15 days: *D. nigrior:* 11–15 days; *D. discolor:* 16–17 days; *Gyrinus* (Wesenberg-Lund, 1913, p. 239) : 14 days; *Gyrinus:* 10–12 days.

Larvae: Gyrinid larvae are distinguished from other coleopterous larvae by their two tarsal claws (in common with other Adephaga, MacGillivray, 1903, p. 289), and the presence of a pair of slender lateral filaments, said to be tracheal gills, on each of the first eight abdominal segments and two pairs on the last segment, one of which Fowler (1912, p. 66) says may be regarded as cerci.

Young *Dineutus* larvae feed by sucking, though Wesenberg-Lund (1915, p. 304) reports that this is not the case with *Gyrinus.* It was my practice to feed the larvae with small tubificid worms, and frequently I found remains of worms from which all internal parts were missing, leaving only the transparent cuticula. In a

similar fashion the young larvae would attack and suck their fellows. Wilson (1923, p. 250–251) records an instance where large numbers of partly grown *Dineutus* larvae were seen attacking young catfish. Newly hatched *Dineutus* larvae run about like caterpillars over the leaves of the aquarium plants. They hold their mandibles wide open to snap hold of anything that came their way. They were cannibalistic to a marked degree, and were apparently alert to their danger, for, when two would approach each other, one would snap at the other, or they would engage in mutual snapping, and then avoid each other quickly and move apart. First instar larvae are practically helpless if caught in the surface film.

The following table to larvae is based on published descriptions and figures. It is obviously tentative, and the characters are probably of much wider application than indicated.

Table to Known Gyrinid Larvae.

(Kuhnt, 1913, p. 1078–1079; Wesenberg-Lund, 1915, p. 305; Wilson, 1923, p. 268.)

A. Clypeus toothed.

B. Clypeus with three teeth; mandibles without teeth on inner margin ..... *Dineutus.*

C. First two pairs of lateral filaments not plumose in mature larvae; mature larva 25–30 mm. long (Wilson, 1923, p. 303, fig. 84).
D. (*Cyclinus*) *americanus* L.

CC. Mature larva apparently with all lateral filaments plumose; 13 mm. long (Nowrojee, 1912, p. 177, pl. xxvi, fig. 5).
D. (*Cyclous*) *unidentatus* Aube.

BB. Clypeus with two or four teeth; lateral filaments all plumose; mandibles with teeth on inner margin.
Gyrinini.

D. Clypeus with four teeth; lateral filaments on penultimate segment longer than the others (Kuhnt, 1913, p. 1074, fig. 36; Reitter, 1908, pl. 40, fig. 5a).
Aulonogyrus striatus Ol.

DD. Clypeus with two teeth; lateral filaments of equal length (Miall, 1895, p. 37, fig. 2).
Gyrinus marinus Gyll.

AA. Clypeus without teeth; lateral filaments of equal length, shorter, broader, and more thickly plumose than *Gyrinus*

(Régimbart, 1882, pl. II, fig. 21; Kuhnt, 1913, p. 1074, fig. 35. Kuhnt's figure, probably through error, shows only nine pair of lateral filaments).

Orectochilus villosus O. Mull.

Pupation: The larvae come to shore to build their pupal cases whence they emerge in a few days. (*Dineutus:* Nowrojee, 1912, p. 178; Wilson, 1923, p. 305–306; *Orectochilus:* Fowler, 1912, p. 66; Lesne, 1902, p. 85–86; *Gyrinus:* Wesenberg-Lund, p. 305; *cf.* Leprieur, 1881, p. LVIII.)

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Summary.

1. The Gyrinid imagoes have the general aquatic adaptations of dytiscids, and, in addition, possess these peculiar features that are probably correlated with their existence at the surface of the water: (1) laterally compressed legs, the meso- and metapods natatorial, (2) a divided eye, (3) an auricular antennal pedicel.

2. The habitat of the imagoes is the surface of fresh water, either standing or slowly flowing, and never very far from vegetation. They are gregarious. The gyrating movements are a fright reaction, since, normally, they swim quite slowly.

3. Copulation takes place on the water (*Dineutus, Gyrinus*) or on shore (*Orectochilus*). Eggs are laid on plants under water.

5. The larvae are predaceous, and their habitat seems to be submerged vegetation, not far from shore, where they go to pupate, but independent of the surface.

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